Surface, Planktonic, and Benthic Foraging by Juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) in Turbid Laboratory Conditions

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We investigated the effect of turbidity on the foraging behaviour of juvenile chinook salmon (*Oncorhynchus tshawytscha*) in the laboratory. We assessed visual ability by measuring the reaction distance of juvenile chinook to planktonic adult *Artemia* prey. Chinook exhibited a log-linear decline in reaction distance with increasing turbidity. These results were similar to those obtained by workers for other species. We also determined the effect of turbidity on the foraging rate of juvenile chinook for surface (*Drosophila*), planktonic (*Artemia*), and benthic (*Tubifex*) prey across a range of turbidity levels (<1, 18, 35, 70, 150, 370, 810 NTU). Foraging rates were reduced at higher turbidities for all three prey. However, for surface and benthic prey, foraging rates were also low in clear water, while highest rates were attained at intermediate turbidity levels (35–150 NTU). We suggest that increased feeding rate in turbid conditions reflects a reduced potential risk to predators.

Nous avons étudié l'effet de la turbidité sur le comportement de recherche de la nourriture chez les juvéniles du saumon quinnat (*Oncorhynchus tshawytscha*) en laboratoire. Nous avons évalué leurs facultés visuelles en mesurant la distance pour obtenir une réaction de quinnats juvéniles à des *Artemia* adultes planctoniques qui servaient de proies. La distance de réaction variait à l'inverse de la turbidité selon une forme semi-logarithmique. Ces résultats sont semblables à ceux obtenus par d'autres chercheurs qui travaillaient sur d'autres espèces. En outre, nous avons déterminé l'effet de la turbidité sur le taux de prédation des quinnats juvéniles qui se nourrissaient de proies de surface (*Drosophila*), planctoniques (*Artemia*) et benthiques (*Tubifex*), en fonction de différents niveaux de turbidité (<1, 18, 35, 70, 150, 370, 810 UTN). Peu importe le type de proie, plus l'eau était trouble, plus le taux de prédation était bas. Toutefois, dans le cas des proies de surface et benthiques, le taux de prédation était bas aussi dans l'eau limpide, alors que le taux le plus élevé a été obtenu dans des conditions intermédiaires de turbidité (35–150 UTN). Nous avançons l'hypothèse à l'effet que l'accroissement du taux de prédation dans des conditions moyennes de turbidité correspond à des risques réduits que les quinnats soient eux-mêmes victimes de prédateurs.

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Underwater images are generally poor in quality, due to the high degree of light attenuation in most aquatic systems (Duntley 1963). Despite this environmental characteristic, most fish species depend on vision for much of their sensory input (Guthrie 1986). In conditions of elevated turbidity, the scattering of light signals is especially acute. Visual range declines precipitously as a function of particle concentration (Duntley 1943; DiToro 1978). The ability to identify and capture prey is proportional to visual range (Vinyard and O'Brien 1976; Confer et al. 1978; Li et al. 1985). Consequently, the foraging rate of fish should decline with increasing turbidity. Several experimental investigations have demonstrated strong negative effects of turbidity on the foraging success of numerous fish species (Gardner 1981; Johnston and Wildish 1982; Sigler et al. 1984; Berg and Northcote 1985; Breitburg 1988). Also, a large body of evidence from field investigations exists purporting the negative effects of turbid water on visually foraging fish species (e.g. Ellis 1936; Buck 1956; Alabaster 1972; Eccles 1986; Hart 1986; McLeay et al. 1987; Simenstad 1990).

Despite the above evidence, juveniles of many marine and anadromous fish species, including salmonids, are often numerous in estuaries having high concentrations of suspended sediment (Blaber and Blaber 1980; Levy and Northcote 1982; Simenstad et al. 1982; Cyrus and Blaber 1987a). Juveniles of several species of fish have been shown to actively prefer turbid over clear water (Cyrus and Blaber 1987b). Juvenile chinook salmon (*Oncorhynchus tshawytscha*) have been shown to occupy turbid estuaries for a significant portion of their early life (Levy and Northcote 1982; Simenstad et al. 1982). In the Fraser Estuary, the residency time of individual juvenile salmon also corresponds to the period of peak river discharge and highest turbidity level (Levy et al. 1979; Levy and Northcote 1982; Servizi and Gordon 1989).

Most experimental work on the effects of turbidity on the feeding behaviour of fish has been done on species which primarily consume planktonic prey. Crowl's (1989) investigation of the reaction distance of largemouth bass (*Micropterus salmoides*) to crayfish and Moore and Moore's (1976) study of prey selectivity by European flounder (*Platichthys flesus*) represent important exceptions. Ware (1973) predicted that increasing turbidity would decrease the feeding rates of fish that consume epibenthic prey because of the decreased contrast of

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the latter with the substrate; however, these predictions have been largely untested. In addition, no studies have been published on surface foraging by fish in turbid conditions.

Juvenile chinook can best be described as generalist foragers (Keast 1979), feeding on a variety of prey types (Levy et al. 1979; Healey 1982; Simenstad et al. 1982). The effect of turbidity on surface, planktonic, and benthic foraging behaviour may be dissimilar. In the present study, we examined the effect of turbidity on foraging rates of juvenile chinook for surface, planktonic, and benthic prey. We considered two components of foraging behaviour: visual ability and foraging rate. To assess visual ability, we determined the reaction distance (a behavioural measure) of chinook to planktonic prey in turbidity conditions up to 230 nephelometric turbidity units (NTU). We assessed foraging rate of juvenile chinook on surface, planktonic, and benthic prey over turbidity levels ranging from <1 to 810 NTU.

Methods

Turbidity

Sediment for this study was obtained from a tidal marsh in the south arm of the Fraser River Estuary, at Ladner, British Columbia. Approximately 10 L of this sediment was sieved through a 0.40-mm sieve to remove larger detritus and then suspended in 125 L of freshwater in a plastic bucket and allowed to settle for a period of 2 h. After this time, the supernatant (75 L) was transferred to another bucket and allowed to settle for a further 48 h. The excess water was then poured off, and the remaining sediment slurry was autoclaved for 30 min. This slurry was added to appropriate aquaria in predetermined amounts.

The relationship between the known concentration of suspended sediment (milligrams per litre) and NTUs measured in experiments is indicated in Fig. 1A. Sediment particles were classified as "subrounded", using the criterion of Muller (1967). Particle sizes ranged from <2 to 25 μm in diameter (≈90% ≤5 μm).

During experiments, turbidity levels were determined from samples taken while tanks were being drained (foraging rate experiments) or from the averages of samples taken immediately before and after observations (reaction distance determinations). These determinations were made with a Fisher 400 DRT turbidimeter, measuring NTUs. Light levels were measured with a LICOR 185-A light meter with a quantum sensor. Illumination at the water surface of the aquaria was $\approx 16.5\ \mu E \cdot m^{-2} \cdot s^{-1}$ (≈850 lx, i.e. the light intensity of a dull day), while light levels measured at the bottom (37.5 cm depth) ranged from <0.01 to $11.5\ \mu E \cdot m^{-2} \cdot s^{-1}$ at corresponding suspended sediment levels from 400 $mg \cdot L^{-1}$ down to <1.0 $mg \cdot L^{-1}$ (i.e. 370 to <1 NTU), respectively (Fig. 1B).

Juvenile Chinook Salmon

Juvenile chinook used in this study were from the Harrison River stock. The Harrison River is a tributary of the Fraser River ≈100 km upstream from its mouth. Harrison chinook begin their seaward migration as underyearling fry and probably spend several months in the turbid tidal channels of the Fraser Estuary after leaving their natal stream.

Chinook were obtained as 0.8-g individuals from a hatchery on the Chehalis River, a tributary of the Harrison River, and transferred to holding facilities at the University of British Columbia. Fish were held in one of two 1000-L holding tanks

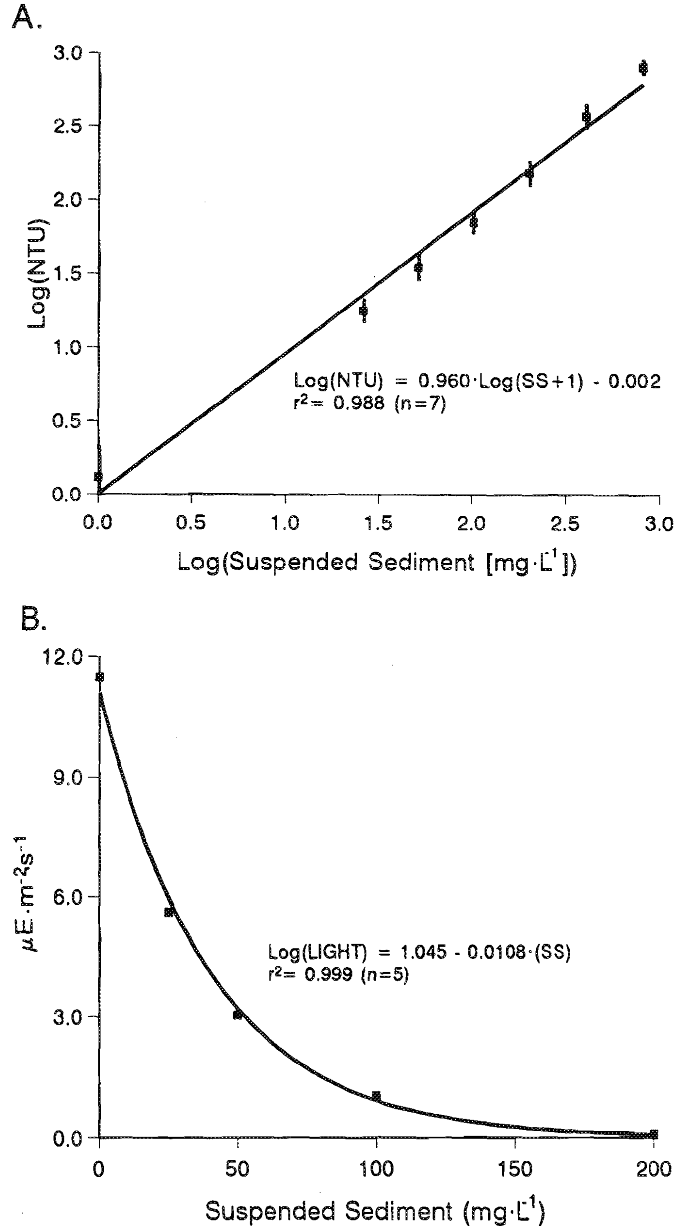

FIG. 1. Relationship of the suspended sediment concentration used in foraging rate experiments with measures of light transmission: (A) turbidity (with SE) and (B) light energy (measured at the aquarium bottom; see Fig. 2 (37.5 cm depth); $1\ \mu E \cdot m^{-2} \cdot s^{-1} \approx 51.2$ lx).

at 6.0–10.5°C under a light regime of 14 h light : 10 h dark. The lights were turned on at 08:00. The water supply (City of Vancouver, <1 NTU during experiments) was treated with 5–20 $mg \cdot L^{-1}$ sodium thiosulphate to absorb free chlorine. Chinook were fed Oregon Moist Pellets (OMP) twice daily (10:00 and 20:00) with amounts required to maintain a growth rate of ≈10% $weight \cdot wk^{-1}$ in the 8–12 wk prior to their use in experiments.

Juveniles used in the determination of foraging rate ranged in mean size from 60 to 70 mm fork length (FL). During any particular experimental run, fish of similar size were used (±3 mm SD). The range of fish sizes used during these investigations was within that observed among wild fish in the field (35–75 mm FL, Levy and Northcote 1982).

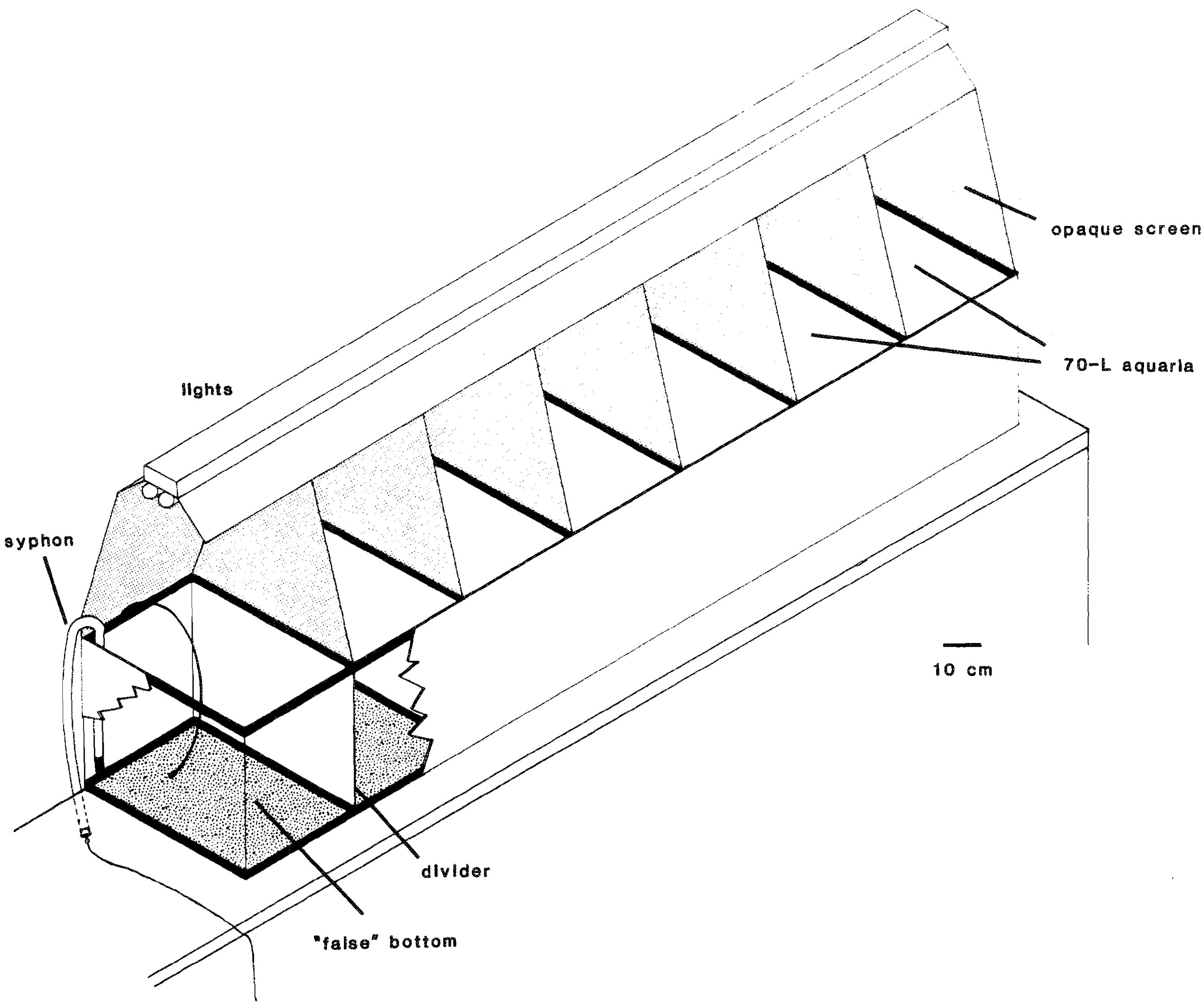

FIG. 2. Aquarium array used for determinations of foraging rate.

Reaction Distance to Prey

The reaction distances of juvenile chinook to adult *Artemia* prey were determined using procedures similar to those described by Vinyard and O'Brien (1976) and Confer et al. (1978). All determinations were made in a 200 × 30 × 25 cm Plexiglas tank. A videocamera was used to record observations from a remote location in a fashion similar to that described by Dill (1990). Illumination of 16.2 $\mu E \cdot m^{-2} \cdot s^{-1}$ at the water surface was provided by paired 40-W fluorescent lights.

Individual juvenile chinook were conditioned to strike at prey items over a period of 2 wk. Prey items (live male *Artemia*, 7–8 mm) were introduced individually at a constant release point using a 4.0-mm-diameter glass "prey tube". Fish were required to strike the prey tube to facilitate the release of the contained prey by the observer. The reaction distance was measured from the point where the chinook reacted to the presence of the prey to the point of prey release. This reaction was characterized by the initiation of a distinct, rapid tail beat followed by a constant acceleration toward the prey in the tube, ending with a strike. Observations were considered valid only if fish were further than 60 cm and facing away from the prey tube prior to prey introduction and if the subject did not hesitate during its approach. During trials, "true" introductions were interspersed with one to four "blank" runs, containing no prey. No strikes were recorded in over 1000 blank runs.

We determined reaction distance at seven turbidity levels ranging from 0.5 to 243 NTU. Trials on any given day were made at only one turbidity level. Juvenile chinook were allowed to acclimate to the test turbidity conditions for 2 h before observations began. The order of the daily turbidity levels was randomized with the exception of the first and last day, which were of fish in clear water. No differences were observed between these latter two treatments. The three chinook used measured 64, 65, and 70 mm FL and weighed 2.62, 3.63, and 3.82 g, respectively. Trials were conducted at temperatures of 13–17°C. Fish had not been fed for 22–24 h before observations began. We made a total of 216 separate determinations of reaction distance.

Foraging Rate Experiments

Prey

Drosophila melanogaster, *Artemia salina*, and *Tubifex* sp.

were chosen to represent surface, planktonic, and benthic prey, respectively. Only adult prey were used. *Artemia* and *Tubifex* were both obtained from a retail outlet, and winged, wild-strain *Drosophila* were cultured in the laboratory. The general characteristics of each of these prey animals may be found in Table 1. Both *Drosophila* and *Tubifex* were readily identifiable surface and benthic prey types, respectively. We have observed *Tubifex* as part of the diet of wild Fraser River individuals. *Drosophila* were an acceptable prey because juvenile chinook consume a wide variety of surface insect prey of similar size, including other dipterans. Although larger than zooplankton prey encountered by juveniles in freshwater, *Artemia* were not larger than those encountered in the marine environment and were smaller and less evasive than *Neomysis mercedis*, a mysid shrimp periodically taken by juvenile chinook in the Fraser Estuary (Northcote et al. 1979). No changes in prey behaviour were observed relative to turbidity treatment.

We established prey densities and feeding trial durations for each prey type in a series of preliminary investigations. Initial prey densities were ≈3.5 *Artemia*$\cdot$L^{-1}, ≈5600 *Tubifex*$\cdot$m^{-2}, and 1300 *Drosophila*$\cdot$m^{-2}. Feeding trials were 1.0, 5.0, and 10.0 min in duration, respectively. The number of *Drosophila* used in feeding experiments exceeded instantaneous surface prey densities in the field by as much as 25-fold. However, these numbers were a reasonable approximation of the potential encounter rate, given prey densities and salmon cruising speeds we have observed in the field.

Three days prior to any given experimental trial, we transferred salmon from the holding tanks to one of several 200-L "conditioning" tanks. In these tanks, fish were fed a diet that consisted of equal proportions of the three prey species mentioned above. Chinook were not fed for 18 h prior to any given experimental trial and were presumed to have been hungry.

Apparatus

The experimental array (Fig. 2) consisted of seven 70-L (50 × 34 × 40 cm) glass aquaria enclosed and separated from each other by 8-mm plywood. All inwardly facing plywood surfaces were painted flat white. Lighting was provided by paired 40-W fluorescent lights running the full length of the array, 45 cm above the water surface. The entire array was enclosed in opaque black plastic isolating it from outside visual disturbances. Each aquarium was similarly separated from the other aquaria.

Small amounts of sediment unavoidably settled out at high turbidity levels (particularly ≥370 NTU). Therefore, each aquarium was fitted with a glass false-bottom through which a mud slurry was visible. This modification reduced the effects of background contrast. We provided a 5- to 7-mm layer of clear 2-mm-diameter glass beads as substrate. This allowed the *Tubifex* to burrow (in appropriate experiments) and also permitted the constant background slurry in the false-bottom to remain visible. A 2.5-cm clear syphon hose was clamped in place at one end of each aquarium to permit rapid aquarium draining. Each hose was primed prior to an experimental run and was activated remotely from the front of the array.

Experimental protocol

Ten fish were placed in each aquarium. We added sediment slurry to each of six aquaria to create turbidity levels of 18, 35, 70, 150, 370, and 810 NTU. No sediment was added to the seventh aquarium, which served as a control (<1 NTU). We randomized the order of the treatments and the control within the experimental array. Chinook were allowed to acclimate to the experimental conditions for 1–1.5 h before prey were added. Prey were introduced to each aquarium in the order of its position within the array. Only one prey type was used in each trial.

For experiments using *Tubifex* prey, we allowed the test fish to acclimate in 4-L meshed plastic holding chambers within each aquarium. We added prey to the main body of the aquarium 10 min before beginning the trial. Within 1 min of their introduction to an aquarium, *Tubifex* burrowed into the bead substrate.

Chinook were allowed to feed uninterrupted throughout the duration of a trial. The appropriate syphon was then activated and the tank was permitted to drain (3 min). Fish were then netted and transferred to a 500-mL container with a lethal concentration of tricaine methanesulfonate (MS222) anaesthetic. We then transferred them to sample jars of 5% formalin. When determining chinook foraging rates for *Artemia* prey, we began netting immediately after the 1 min of experimental feeding period had elapsed, using an aquarium electroshocker to facilitate fish retrieval. Although this technique caused feeding to cease, it did not appear to cause regurgitation. The stomach contents of fish from all prey experiments were dissected and either enumerated (*Drosophila* and *Artemia*) or blotted dry and weighed to the nearest milligram (*Tubifex*).

Results

Reaction Distance

The effect of turbidity on the median reaction distance of juvenile chinook to male, adult *Artemia* prey was best described

TABLE 1. Physical and visual characteristics of prey used in determinations of juvenile chinook foraging rates.

Prey	Length (mm)[a]	Weight (mg wet)[b]	Other characteristics
Drosophila	2.5 ± 0.3	0.9	Black and white with red eyes; winged; previously frozen
Artemia	6.7 ± 1.1	5.3	White to pink with red/black eyes; weak swimmers (no developed escape response)
Tubifex	14.8 ± 7.0	1.9	Dark red/black; burrowing; weakly evasive (no effective escape, but longer handling time than other two prey)

[a]Mean ± SD (minimum N = 300)
[b]Batch weighings; mean weight/individual only.

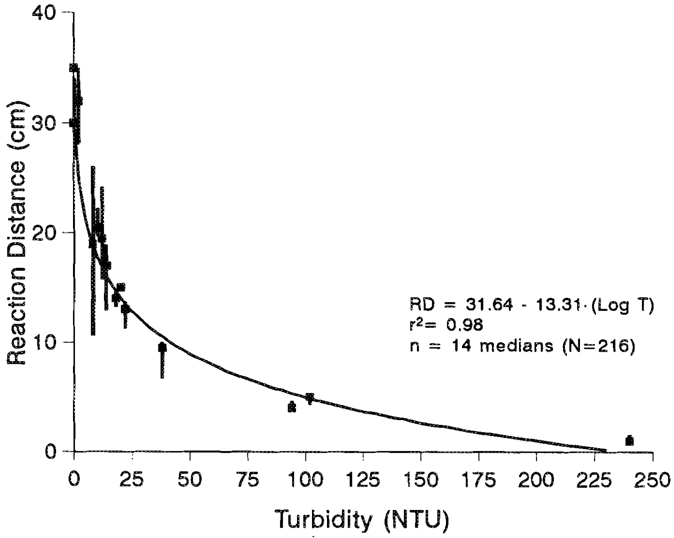

FIG. 3. Effect of turbidity on the reaction distance of juvenile chinook for *Artemia* prey (regression based on median values; bars include 50% of data points).

by the log-linear relationship

$$\mathrm{RD} = 31.64 - 13.31 \times \log T$$

where T = turbidity (in NTUs) and RD = reaction distance (in centimetres) (Fig. 3). An r^2 of 0.98 among the 14 treatment medians supported a high degree of confidence in this relationship ($r^2 = 0.70$ when all data points were analyzed separately). We observed no significant dissimilarities between subjects (ANOVA, $p > 0.05$).

Surface Foraging Rate

For juvenile chinook foraging on *Drosophila* prey, turbidity significantly affected foraging rate (ANOVA, $p < 0.05$). Highest foraging rates, 1.1 prey·min^{-1} (over 10 min), were attained in intermediate turbidity treatments, 35–150 NTU (Fig. 4). Chinook exhibited significantly depressed foraging rates at <1 and 810 NTU (t-test, $p = 0.016$ and $p = 0.004$, respectively). Individual variability was high; some fish consumed 40 prey or more, while many others had empty guts. This high variability was reflected in large standard errors and by the proportion of individuals actively feeding (Fig. 4). The observed relationship represented a marked departure from the foraging rate expected on the basis of the reaction distance of juvenile chinook in turbid conditions (Fig. 3).

Planktonic Foraging

The effect of turbidity on planktonic foraging by chinook on *Artemia* prey was also significant (ANOVA, $p < 0.001$). However, the highest foraging rates, 11.0–15.0 prey·min^{-1} (over 1.0 min), were observed at all low turbidity treatment levels (≤70 NTU), while significantly reduced rates were demonstrated only in the high treatments, ≥350 NTU (Fig. 5). These rates approached zero in the 810 NTU treatments. Foraging rates were not proportional to the percentage of fish actively foraging, which was close to 100% at all turbidity levels tested (Fig. 5). The foraging rates at 810 NTU were significantly lower than those at turbidity levels below 150 NTU (Tukey test, $p < 0.001$). Foraging rates on planktonic *Artemia* prey by chinook juveniles were more consistent than those dem-

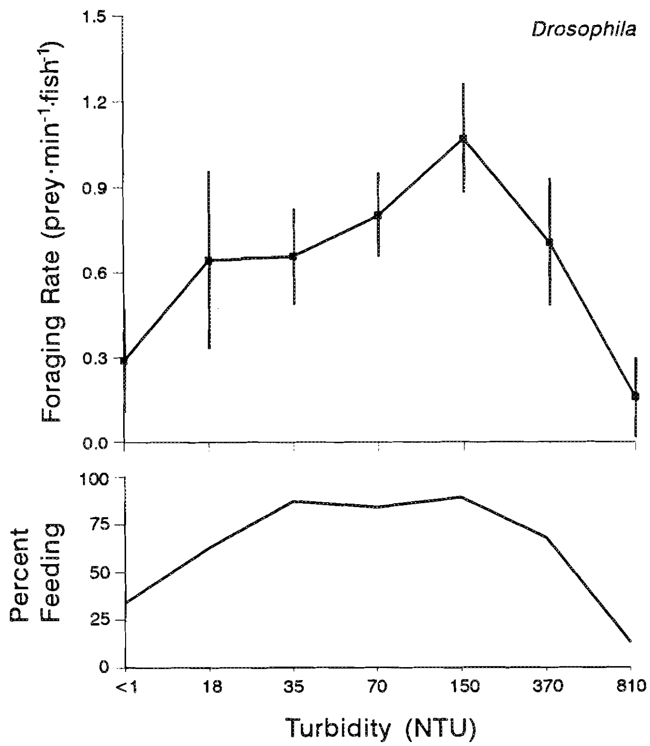

FIG. 4. Effects of turbidity on mean foraging rate of juvenile chinook feeding on surface prey (*Drosophila*) and the percentage of salmon foraging in 70-L aquaria in 10.0-min trials (vertical bars indicate the standard error of means from five trials).

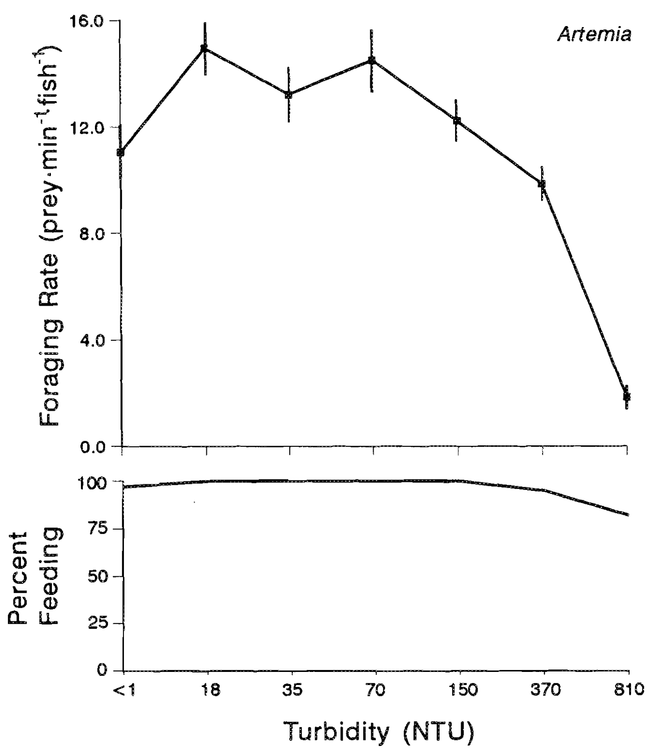

FIG. 5. Effects of turbidity on mean foraging rate of juvenile chinook feeding on planktonic prey (*Artemia*) and the percentage of salmon foraging in 70-L aquaria in 1.0-min trials (vertical bars indicate the standard error of means from five trials).

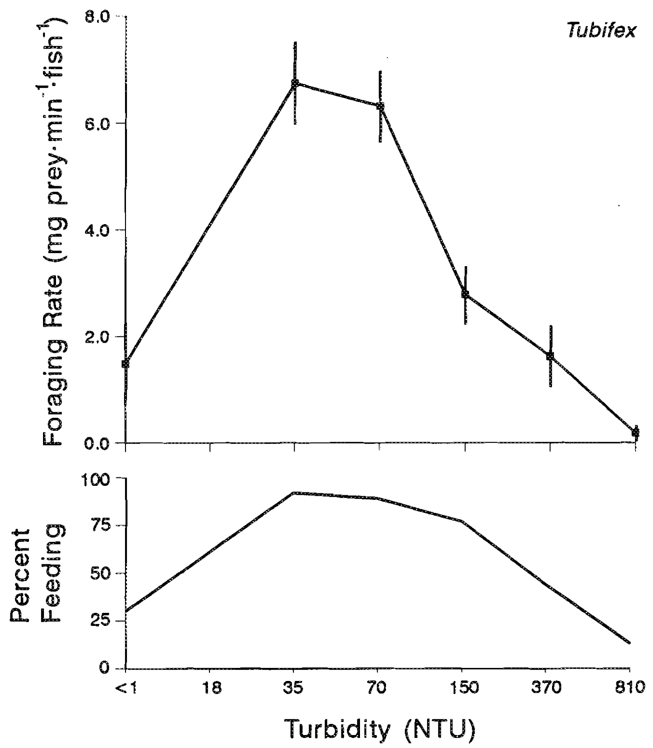

FIG. 6. Effects of turbidity on mean foraging rate of juvenile chinook feeding on benthic prey (*Tubifex*) and the percentage of salmon foraging in 70-L aquaria in 5.0-min trials (vertical bars indicate the standard error of means from five trials).

onstrated for surface foraging, with lower variance among and within means.

The "high to low" foraging rate pattern exhibited by these fish with increasing sediment concentration was similar to the expectations based on the visual ability of these fish (Fig. 3). Search time (or search volume – handling time relationships) may have not limited the foraging rate at turbidity levels below 150 NTU, possibly explaining the asymptotic nature of the relationship at lower treatment levels.

Benthic Foraging

Benthic foraging rates on *Tubifex* prey followed the same generalized pattern as that demonstrated by surface foraging chinook. Turbidity had a significant effect on foraging rates (ANOVA, $p < 0.001$). The highest foraging rates were demonstrated at intermediate turbidities, 35–150 NTU, whereas reduced foraging rates were observed at the lowest and highest treatment levels (Fig. 6). Peak mean foraging rates were >6.0 mg prey·min^{-1} (over 5.0 min). Multiple comparisons revealed that differences in foraging rates between intermediate and both high and low turbidity levels were significant (Tukey test, $p < 0.01$). Foraging rates were loosely reflected by the proportion of fish actively foraging at each treatment level (Fig. 6). As for surface feeding behaviour, the foraging relationship we observed for benthic prey again represented a marked departure from the foraging rate which might be predicted from the reaction distance of juvenile chinook in turbid conditions (Fig. 3).

Discussion

Turbidity has often been viewed as detrimental to the foraging activities of fishes (Ellis 1936; Alabaster 1972; Gardner 1981; Bruton 1985), especially salmonids (Confer et al. 1978; Sigler et al. 1984; Berg and Northcote 1985). This concern has been justified. Suspended sediment can be deleterious to salmonid feeding rates, growth, and survival (Servizi and Martens 1987; Newcombe and MacDonald 1991). However, these responses to chronic exposure generally occur only at levels beyond those experienced naturally (Wallen 1951).

In the face of the above evidence, several studies demonstrate that fishes, especially larval and juvenile forms, may actively seek out turbid waters in the field (Bruton 1979; Blaber and Blaber 1980; Cyrus and Blaber 1987a). The active preference of turbid over clear conditions has been demonstrated in the laboratory for the juveniles of several species (Gradall and Swenson 1982; Cyrus and Blaber 1987b).

The effect of turbidity on foraging behaviour has not been demonstrably consistent. Although many studies have demonstrated that suspended sediment has a deleterious effect on the foraging rate of fish (for review, see Bruton 1985), many of these investigations did not demonstrate significant effects at low turbidity levels (Heimstra et al. 1969; Johnston and Wildish 1982; Breitburg 1988). In fact, Boehlert and Morgan (1985) and Vandenbyllaardt et al. (1991) described increases in planktonic foraging rate by larval Pacific herring (*Clupea pallasi*, previously *Clupea harengus pallasi*) and piscivory by young walleye (*Stizostedion vitreum*) in turbid conditions, respectively. Moore and Moore (1976) reported a shift in the foraging pattern or prey preference in turbid conditions, suggesting behavioural flexibility.

Suspended sediment can have a deleterious effect on visual ability in fishes. The relationship we observed between turbidity and reaction distance of juvenile chinook to *Artemia* prey was similar in form to those described for bluegill (*Lepomis macrochirus*) (Vinyard and O'Brien 1976) and lake trout (*Salvelinus namaycush*) (Confer et al. 1978). Reaction distance declined log-linearly with increasing turbidity for all these species. The probability of prey detection has been shown to be proportional to the reaction distance of fish (Ware 1973; Confer and Blades 1975; Hairston et al. 1982). Therefore, the observed decline in reaction distance we describe suggests that the probability of prey detection should also be reduced in turbid conditions.

Visual ability alone cannot fully explain the foraging behaviour of juvenile chinook. Established theory concerning optical constraints (Duntley 1963; DiToro 1978) seems to explain the rates we demonstrated for planktonic foraging by chinook. We observed high foraging rates at low turbidity and much reduced rates at elevated levels (>150 NTU). The decline in foraging rate may have been more distinct, similar to that demonstrated by Gardner (1981) for bluegill, except that prey handling time probably constrained the expression of foraging rate by individuals in clearer water. However, this explanation is untenable for surface and benthic prey. An hypothesis based solely on visual effects is unlikely to predict the increased foraging rates we observed at intermediate turbidity levels as compared with clear water conditions.

A revision in our thinking about foraging behaviour in turbid water is required. Boehlert and Morgan's (1985) explanation for elevated feeding rates in larval Pacific herring in turbid conditions involved the enhancement of visual contrast. They maintained that rotifer prey were effectively silhouetted against the constant background illumination afforded by the light-scattering sediment particles. Work on contrast perception in fish (Hester 1968) and its effect on foraging behaviour (Ware 1973) suggests that this may be possible. T. Godin and R. S.

Gregory (unpubl. data) demonstrated that juvenile chinook respond faster to prey against turbid backgrounds than in clear conditions, also suggesting such an explanation. Although such work suggests that contrast enhancement is possible, we do not believe it provides a complete explanation for the trends we have observed. Conceivably, contrast enhancement would enable planktonic prey to be more quickly recognized. However, the same cannot be said of benthic or surface prey. Benthic prey could only be better contrasted if turbidity acted to modify the substrate characteristics. Turbid environments tend toward a uniform grey–brown background, but this is unlikely to change appreciably in varying turbidity phases in a given system. In our experiments, we have controlled for this effect. Surface prey cannot assume higher contrast in turbid water because the sky provides background illumination independent of turbidity. Alternately, Vandenbyllaardt et al. (1991) suggested that differential retinal development between piscivorous walleye and their minnow prey makes foraging in turbid water more successful for the predator. In our experiments, we selected prey that were nonevasive, eliminating this as a factor. Another explanation is required to fully elucidate juvenile chinook foraging behaviour in clear and turbid conditions.

We suggest that behavioural flexibility by chinook is responsible for the variable form and magnitude of the effect of turbidity on foraging rate. In clear water, chinook may forage on benthic or surface prey at a reduced rate, sacrificing the obvious energetic reward for some other gain, possibly the reduction of potential exposure to predation risk (Dill 1983). The size-selective nature of predator-induced mortality in young salmon has long been known (Parker 1971). We suggest that turbidity may act as a form of cover, reducing the perception of risk in juvenile chinook. However, at high turbidity (>150 NTU, present study), visual ability becomes substantially impaired and foraging ability is reduced regardless of any concurrent gains.

The act of foraging has been increasingly viewed as an inherently dangerous activity for many animals (Lima and Dill 1990). A foraging fish will be more visible to a potential predator in clear water than in turbid water. Also, a moving, foraging fish is more likely to be detected by a predator than a stationary, vigilant one (Donnelly and Dill 1984). We suggest that juvenile salmon are sensitive to this potential risk and may forage accordingly. Gregory (1993) has shown that juvenile chinook may reduce their predator avoidance behaviour in turbid conditions. Higher foraging rates may be realized at less "risk-prone" but poorer visibility conditions.

When we consider chinook foraging behaviour toward planktonic *Artemia* prey, the above explanation must be expanded. Higher foraging rates were observed at intermediate turbidity levels for fish foraging on either surface or benthic prey. This pattern was not observed for chinook foraging on plankton. *Artemia* prey were ingested at relatively high rates at both low and intermediate turbidity levels (i.e. all turbidity treatments ≤150 NTU). The apparent dissimilarity in the forms of these relationships, between planktonic foraging on the one hand and both surface and benthic foraging on the other, may be explained if it is considered that chinook may exhibit a prey- or microhabitat-specific sensitivity to potential predation risk. Behaviours consistent with such a pattern have been described (Lima and Dill 1990).

The results we have presented here, and those of Boehlert and Morgan (1985), Vandenbyllaardt et al. (1991), and Neverman and Wurtsbaugh (1992), demonstrate increased foraging rates in visually restricted conditions. We have also observed similar results among wild pink (*O. gorbuscha*), chum (*O. keta*), and chinook salmon (R. S. Gregory, unpubl. data). These findings suggest a trade-off between visual ability and some other variable, although Vandenbyllaardt et al. (1991) suggested a univariate explanation. We believe that in all four cases, perceived risk of predation was the additional variable. Although Boehlert and Morgan's (1985) contrast enhancement hypothesis cannot be entirely dismissed, a predation-averse behavioural explanation is also possible. Giguere and Northcote (1987) have demonstrated that full guts in otherwise transparent *Chaoborus* larvae increased both their visibility and the likelihood of their being preyed upon by fish. However, a similar "cost" of increased foraging rates (i.e. in terms of increased risk of predation) in herring would be reduced in turbid water. The visual contrast of a full gut, and the commensurate risk of predation, would be lower in turbid than in clear water. Similarly, Neverman and Wurtsbaugh (1992) observed that peak foraging rates by young-of-the-year sculpin were highest at intermediate light levels, while they were reduced at both higher and lower light levels. We suspect a similar trade-off in their results also. However, Gregory (1991) suggested that light levels are a poor predictor of foraging rate in chinook, except on a coarse scale. While low light levels may reduce the perceived risk in some species (sockeye salmon (*O. nerka*), Clark and Levy 1988; sculpin, Neverman and Wurtsbaugh 1992), turbidity may perform this function in others (tilapia, Bruton 1979; small estuarine fish, Blaber and Blaber 1980 and Cyrus and Blaber 1987a; juvenile chinook, this study).

Although their visual ability may be deleteriously affected by turbid conditions, juvenile chinook may increase their feeding activity because of a reduced potential risk to predators. Salmonids in clear waters tend to exhibit highest foraging rates at dawn and dusk (Adams et al. 1987; Levy 1987; Angradi and Griffith 1990). Our own field observations (unpubl. data) suggest that juvenile salmon in the turbid tidal habitats of the Fraser Estuary forage actively throughout the day, possibly explaining the high growth rates chinook exhibit in these habitats (Levy and Northcote 1982). We suggest that juvenile chinook in this study demonstrated foraging rates consistent with both the visibility of their prey and their potential risk of predation.

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